Biogeographical patterns in the fauna associated with southern African mussel beds

Wendy Hammond & Charles Griffiths*

Centre for Invasion Biology and Marine Biology Research Institute, University of Cape Town, Rondebosch, 7700 South Africa

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Macrofauna communities colonizing intertidal mussel beds were sampled at seven sites between Swakopmund (Namibia) and Salt Rock (KwaZulu-Natal). Mean mussel cover, length, biomass and bed depth were all low in the southeast (former Transkei). Faunal abundance and biomass were minimal along the south coast, increasing up both west and east coasts. Species diversity and richness showed the reverse trends, peaking at south coast sites and dropping off to the west and east. Multivariate analysis grouped the faunal communities into four distinct clusters, corresponding to the recognized Namib, Namaqua, Agulhas and Natal biogeographical provinces. The low mussel biomass and cover in the Eastern Cape can be attributed to intense human exploitation, but the low faunal abundance and biomass along the south coast was unexpected, as was the negative correlation between faunal abundance and diversity. Over recent decades intense exploitation has resulted in marked declines in mussel cover along the east coast, while the *M. galloprovincialis* invasion has resulted in dramatic increases in mussel cover to the west. The results given here indicate how these changes might have affected the wider intertidal communities in these regions.

Key words: biogeography, South Africa, mussels, invasive species.

INTRODUCTION

Five mussel species are common along the southern African coastline, defined here as extending from the Cunene River (17°20′S, 11°40′E), on the border of Namibia and Angola, to the southern border of Mozambique (26°S, 2°E), a distance of some 4500 km. The brown mussel *Perna perna* is the dominant species on the sub-tropical east and warm-temperate south coasts, is absent along the west coast of South Africa, then reappears in Namibia. The indigenous black mussel *Choromytilus meridionalis* and ribbed mussel *Aulacomya ater,* as well as the introduced Mediterranean mussel *Mytilus galloprovincialis,* are all abundant in the cooler waters of the South African west coast, but extend along the south coast to varying extents (Fig. 1). The smaller *Semimytilus algosus* is abundant only in central to northern Namibia, where it has been introduced, probably from South America (Van Erkom Schurink & Griffiths 1990).

Beds of these and other mussel species create complex secondary habitats that offer a diversity of niches, including the shell surfaces of the mussels themselves, the complex web of byssal threads that attach them to the substratum and to one another, and the sediment and biodeposits that accumulate within and below the mussel matrix (Suchanek 1992). As a result, mussel beds typically support a dense and diverse assemblage of associated invertebrates (Suchanek 1985; Lintas & Seed 1994). The communities colonizing mussel beds in the South African region have received relatively little attention. Hockey & van Erkom Schurink (1992) and Griffiths *et al.* (1992) compared the fauna colonizing *M. galloprovincialis* and *A. ater* beds on the west coast of South Africa, Hammond (2001) investigated the effect of tidal elevation, mussel species and mussel size on the fauna and Hammond & Griffiths (2002) examined the effects of wave exposure on these communities.

In this study we investigated how the mussel-bed fauna around southern Africa varies geographically in terms of abundance, biomass and species composition. We also tested whether the patterns within this single, relatively consistent habitat follow those recognized for the macrofauna as a whole (note that in previous studies detailed below different habitat types were compared – for example, the kelp beds and limpet-dominated shores of the west with the coral, zoanthid and turf dominated ones in the east). Stephenson (1948) divided the southern African coast into three marine provinces: an East Coast Province extending from Mozambique to Port St Johns, a South Coast Province from Port St Johns to Cape Point and a West Coast Province from Cape Point to Walvis Bay (Namibia). More recently

*Author for correspondence. E-mail: clgriff@pop.uct.ac.za

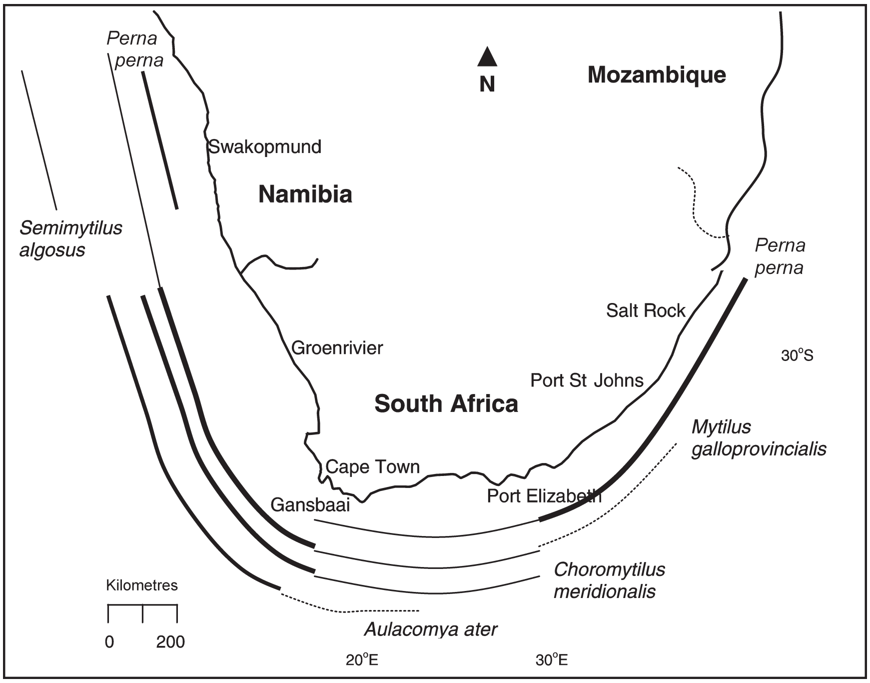

Fig. 1. Map of southern Africa showing the location of sampling stations and the distribution of the dominant mussel species. The thickness of lines indicates relative abundance.

Emanuel *et al.* (1992) modified this system and proposed five major provinces on the basis of a cluster analysis of invertebrate data. These are a Cool Temperate North West Coast (Namib) Province; a Cool Temperate South West Coast (Namaqua) Province; a Warm Temperate South Coast (Agulhas) Province; and a Subtropical East Coast (Natal) Province, which is in turn separated from a tropical Delagoa Province at approximately Cape Vidal.

Since mussel beds represent important habitats for intertidal invertebrates, we hope our results will also shed some light on the consequences of the rapid changes that are occurring in the prevalence of mussels along the southern African coastline. Over the past few decades there has been an enormous increase in mussel biomass and cover along the west coast of South Africa and a corresponding decrease along the east coast. The reasons for these changes are the arrival and proliferation of the invasive *M. galloprovincialis* on the west and south coasts (Hockey & van Erkom Schurink 1992; Griffiths *et al.* 1992; Branch & Steffani 2004; Robinson *et al.* 2005) and human exploitation of *P. perna* on the east coast (Hockey & Bosman 1986; Lasiak & Dye 1989; Lasiak 1991; Lasiak & Barnard 1995; Lawrie & McQuaid 2001) where up to 82.7 g/m^2 (wet-weight) of mussels can be removed per year by local people (Siegfried *et al.* 1985). As a result there has been an overall reduction of mussel biomass and cover on the high shore in these regions. Rates of mussel recruitment are also greatly reduced (Harris *et al.* 1998), making it unlikely that stocks will recover rapidly, even if exploitation rates decline. Although these trends are well established, the consequences of the changes in mussel cover on the wider invertebrate community have not previously been evaluated.

MATERIALS & METHODS

Data were collected at seven locations between Swakopmund (Namibia) and Salt Rock (KwaZulu-Natal) during 2000 and 2001. At each location three sampling sites were selected, separated by distances of hundreds of metres and each containing large beds of the dominant mussel species in the region. At each site percentage mussel cover was estimated by placing 50 × 50 cm quadrats at 10 random points within the lower littoral zone, and estimating mussel cover within each. Mussels and their associated fauna were then removed from three randomly placed 10 × 10 cm quadrats in this zone, using a paint scraper dug under the mussel matrix. Samples were placed in marked plastic bags

Table 1. Dominant mussel species, mean percentage cover, mussel length, wet mussel biomass and mussel-bed depth at each sampling location (standard errors in brackets).

Site	Dominant species	Mussel cover (%)	Mussel length (mm)	Mussel biomass (kg/m^2)	Mussel-bed dept (cm)
Swakopmund	*P. perna*	61.8 (± 34)	53.5 (± 6.3)	42.3 (± 22.8)	5.1 (± 1.6)
Groenrivier	*M. galloprovincialis*	77.1 (± 14)	46.9 (± 6.5)	17.7 (± 4.6)	5.5 (± 0.8)
Cape Town	*M. galloprovincialis*	67.9 (± 35)	51.7 (± 9.3)	25.9 (± 4.1)	5.6 (± 0.6)
Gansbaai	*C. meridionalis*	77.5 (± 22)	47.1 (± 4.2)	55.8 (± 7.9)	5.0 (± 0.9)
Port Elizabeth	*P. perna*	32.2 (± 15)	42.0 (± 6.2)	17.9 (± 5.9)	4.6 (± 1.2)
Port St Johns	*P. perna*	2.4 (± 2)	30.9 (± 5.5)	4.8 (± 2.2)	1.9 (± 0.6)
Salt Rock	*P. perna*	56.6 (± 32)	49.5 (± 8.5)	39.0 (± 14.1)	5.1 (± 0.9)

for further analysis. Mussel-bed depth was recorded for each quadrat by placing a ruler horizontally across the removed section and measuring its height above the rock surface. The weight and length of the mussels were recorded using a spring balance and vernier callipers, respectively. Macrofaunal species were identified to species level as far as possible and counted under a dissecting microscope; meiofauna (<1 mm) were not analysed. Representative wet weights were established by weighing 10 random individuals of each species and used to establish the total faunal biomass for each sample.

A one-way ANOVA (95%) was used to analyse differences in percentage mussel cover, mussel-bed depth, mussel length and mussel biomass among sampling sites and to compare faunal abundance, biomass, species diversity (Shannon-Wiener index H') and species richness (Margalef's index d') among sites. Significant results were followed by Tukey tests. All univariate statistical analyses were conducted using Statistica (version 2001).

A two-way-nested ANOSIM test, reflecting the differences between groups of samples, was performed on the Bray-Curtis similarity matrix of faunal abundance and biomass. Sites were grouped *a priori* to be representative of the different locations, with replication samples taken within locations. A Bray-Curtis similarity matrix was constructed for the abundance and biomass data sets, transformed using a fourth-root transformation. A one-way ANOSIM was then performed on these data. Dendrograms were constructed and, in addition to classification, data were subjected to multidimensional scaling (MDS). To detect which species were responsible for the different dominance patterns within communities at different locations, an analysis of the contribution by individual species to the overall similarity measure, SIMPER (Similarity Percentages) was performed. All multivariate and univariate community analyses were done using PRIMER 5 (Plymouth Routines in Multivariate Ecological Research).

RESULTS

Table 1 lists the characteristics of the mussel beds sampled at each location. The dominant mussel species in Namibia and all along the south and east coasts of South Africa was *P. perna,* while on the west coast of South Africa it was *M. galloprovincialis. C. meridionais* dominated at only one site, Gansbaai. Mussel cover, mean mussel length, biomass and bed-depth were all extremely variable between sites, with little systematic geographical tendency in the results. All measures, were, however, greatly lower at Port St Johns, where mussel cover was only 2.4% (compared to 32–77.5% at other sites), average mussel biomass 4.8 kg/m^2 (compared to 17.7–55.6 kg/m^2 at other sites) and mussel-bed depth 1.9 cm (compared to 4.6–5.6 cm at other sites).

The characteristics of the faunal communities at the sample locations are given in Table 2. Again there was great variation between and indeed within sites. The highest average faunal abundance by far (23 670 m^2) was found at Salt Rock, with sites along the west coast showing intermediate densities (10 890–14 780 m^2) and those along the south coast lower densities 3490–9510 m^2 (Table 2). Average faunal biomass showed a similar pattern, with Salt Rock having a biomass (6.7 kg/m^2) almost double that of any other site, and sites on the south coast having the lowest faunal biomass values.

In total 114 faunal species were recorded across all locations, with the highest number recorded at a single location being 42 at Port Elizabeth and the lowest number 21 at Gansbaai. Complete lists of the species found at each site, plus their densities and biomass are given in Hammond (2001). Faunal

Table 2. Abundance, wet biomass, species diversity (Shannon-Wiener index) and species richness (Margalef's index) of macrofaunal communities at each sampling location (standard errors in brackets).

Sites	Macrofaunal abundance (no/m^2)	Macrofaunal biomass (kg/m^2)	Total macrofaunal species	Diversity (*H'*)	Richness (*d'*)
Swakopmund	14780 (±8006)	3.6 (±3.7)	37	1.4 (±0.2)	1.6 (±0.3)
Groenrivier	10890 (±10072)	2.5 (±2.3)	34	1.6 (±0.2)	2.3 (±0.6)
Cape Town	3490 (±1375)	2.4 (±1.9)	30	1.9 (±0.2)	2.4 (±0.4)
Gansbaai	4510 (±2112)	1.2 (±0.5)	21	1.8 (±0.2)	2.3 (±0.3)
Port Elizabeth	4200 (±1221)	1.7 (±0.6)	42	1.8 (±0.3)	2.7 (±0.5)
Port St. Johns	9510 (±3383)	3.8 (±1.2)	42	1.4 (±0.4)	2.4 (±0.5)
Salt Rock	23670 (±14652)	6.7 (±4.6)	32	1.0 (±0.4	1.8(±0.6)

diversity and richness were both lowest at Salt Rock and Swakopmund, with highest values being recorded along the south coast, at those sites at which faunal abundance was lowest (Table 2).

Comparing these two tables, it is of interest to note that there appears to be a negative correlation between mussel cover and species richness, those sites with the lowest mussel cover (Port Elizabeth and Port St John's) having the highest number of species, while that with the highest cover (Gansbaai) has the lowest number of species. Similarly, there is a negative correlation between species diversity and faunal abundance, as depicted in Fig. 2, suggesting that sites supporting large densities of invertebrates do so by virtue of having a few exceptionally abundant species, while less dense communities still retain most of these species.

A similarity dendrogram (Fig. 3), comparing the sites on the basis of abundances of the 114 faunal species recorded, shows that samples from the same localities group tightly together. Two major groupings emerge, with the east coast sites of Salt Rock and Port St Johns separating from all other localities at a similarity of only *c.* 20%. The remaining group can further be divided into a Swakopmund cluster; a Groenrivier, Cape Town and Gansbaai cluster, and a separate Port Elizabeth cluster at a similarity of *c.* 35%. The same trends are apparent when the data are presented in terms of biomass and MDS ordinations for both abundance and biomass data (Hammond 2001, not repeated here) are in agreement with the dendrograms, grouping samples from the same localities into clearly separated clusters.

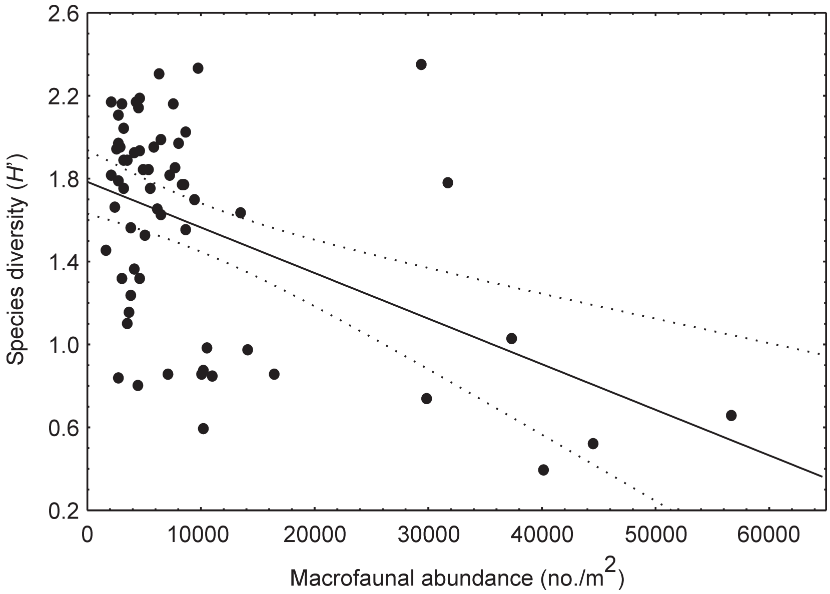

Fig. 2. Species diversity (Shannon-Wiener index *H'*) plotted against infaunal abundance (numbers/m^2) and showing 95% confidence limits $y = -0.00x + 1.78$. $R = -0.47$. $P < 0.05$.

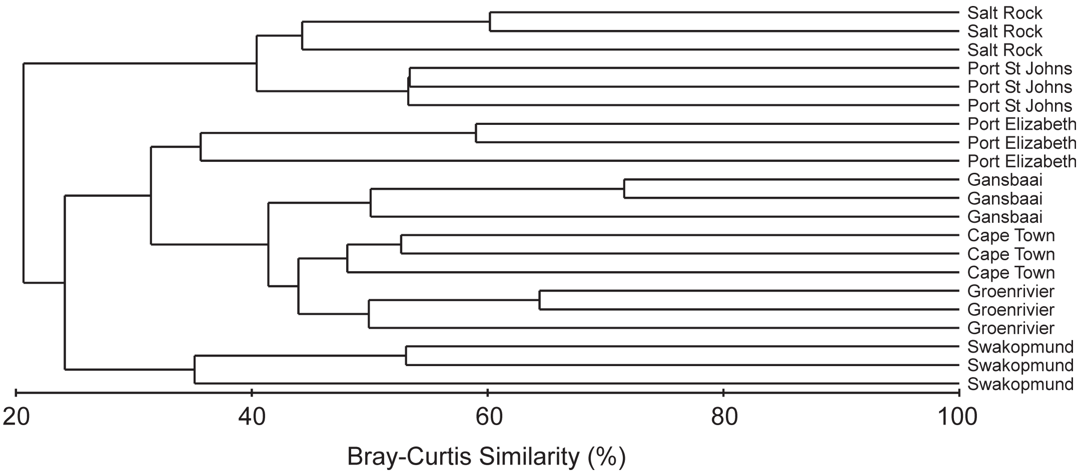

Fig. 3. Dendrogram showing similarity of 21 sites sampled at seven locations, based on the abundances of 114 faunal species recorded.

SIMPER analysis revealed species responsible for characterizing the infauna of the various locations. The most important species characterizing locations in terms of faunal abundance are listed in Table 3. Notable amongst these were the barnacle *Tetraclita serrata,* which was abundant for east coast sites and absent elsewhere (although the species range in fact extends to Namibia). The sea

Table 3. The most abundant macrofaunal species characterizing mussel-bed communities at the various sampling localities. Contribution percentage is the percentile contribution per species to total community abundance.

	Swakopmund	Groenrivier	Cape Town	Gansbaai	P.E.	Port St Johns	Salt Rock
Average similarity (%):	**48.79**	**57.66**	**54.78**	**61.23**	**50.55**	**57.91**	**51.35**
Macrofaunal species	**% Contribution to total community abundance**						
Acanthochiton garnoti					3.70	1.91	
Aulactinia reynaudi	8.50	8.17	3.94	13.58		5.87	15.83
Burnupena lagenaria		4.26		3.80		4.92	
Chthamalus dentatus	3.82						9.71
Discinisca tenuis	9.40						
Dynamenella huttoni		5.00	10.49	9.55			
Eunice aphroditois						9.09	3.39
Exosphaeroma kraussii	4.36						
Fissurella mutabilis			8.34		3.08		
Gunnarea capensis			3.20		3.50		
Helcion dunkeri					11.80	6.23	
Nematodes					7.44		
Nereis spp.						18.43	
Notomastus latericeus				3.79			
Nucella cingulata		18.79					
Octomeris angulosa		6.58					
Orbinia angrapequensis						1.98	
Paramoera capensis		8.19	8.57	12.27	11.44		5.14
Parisocladus perforatus	7.96						
Pomatoleios kraussii						5.60	6.68
Pseudocnella sykion	20.22						
Pseudonereis variegata	27.88	7.20	30.51	24.99	32.93	13.04	7.45
Scutellastra granularis	6.06	20.01	18.44	16.24			
Tetraclita serrata					12.71	20.89	39.01
Thaumastoplax spiralis							3.02
Thelepus spp.			9.48	4.90			
Tricolia neritina				3.51			

Table 4. The dominant species characterizing communities in terms of biomass at the various sampling localities. Contribution percentage is the percentile contribution per-species to the total community biomass.

	Swakopmund	Groenrivier	Cape Town	Gansbaai	P.E.	Port St Johns	Salt Rock
Average similarity (%):	**27.01**	**43.33**	**70.14**	**41.29**	**69.32**	**58.98**	**51.50**
Macrofaunal species	**% Contribution to the total community biomass**						
Aulactinia reynaudi				13.69			
Dynamenella huttoni		9.40					
Nereis spp.						35.38	
Nucella cingulata		24.35					
Paramoera capensis				6.11			
Pseudocnella sykion	21.09						
Pseudonereis variegata	71.77	19.30	86.32	57.63	91.98	8.78	
Scutellastra granularis		39.33	9.68	11.90			
Tetraclita serrata						51.03	90.16
Thelepus spp.				4.84			

cucumber *Pseudocnella sykion* and the brachiopod *Discinisca tenuis* were characteristic of Swakopmund and the whelk *Nucella cingulata* was found only at Groen Rivier. Varying densities of other species, particularly combinations of the abundant limpet *Scutellastra granularis* and polychaete *Pseudonereis variegata* characterized the remaining locations. In terms of biomass, a smaller subset of the generally larger species characterized the various sites, as shown in Table 4.

DISCUSSION

This study examined biogeographic patterns in the composition and biomass of mussel-bed macrofaunal communities around the coast of southern Africa. The dominant mussel species changed from *P. perna* in Namibia, to *M. galloprovincialis* on the west coast of South Africa and then back to *P. perna* on the south and east coasts. Only one of our locations was dominated by *C. meridionalis.* This represents a fairly recent change in dominance pattern, in that prior to the introduction of *M. galloprovincialis* in about 1980, the most important mussel species on the South African west coast would have been *C. meridionalis* and *A. ater.* The west coast now supports a far more extensive cover and greater biomass of mussels than was previously the case (Hockey & van Erkom Schurink 1992; Griffiths *et al.* 1992; Robinson *et al.* 2005). The expansion of this rich community over what was previously largely barren, limpet-dominated rock, must have had profound implications for overall intertidal biomass and community structure, as discussed further below.

Average mussel cover and mean size were fairly consistent across locations, despite the change in species, except at Port St Johns, and to a lesser extend Port Elizabeth, where average cover and mussel size were much lower. This is almost certainly a consequence of the intense exploitation of mussels on the southeast coast (Hockey & Bosman 1986; Lasiak & Dye 1989; Lasiak 1991; Lasiak & Barnard 1995; Lawrie & McQuaid 2001). Further up the coast at Salt Rock, conditions appear to be better, and overall increases in mussel cover, size and biomass was evident. Mussel biomass and bed depth were extremely variable, but again were notably depressed at Port St Johns, due to mussel exploitation.

Faunal abundance and biomass, which have been shown to be independent of mussel species (Hammond 2001), were both high on the Namib and Namaqua coasts, dipping on the south and southeast coasts, and then rose sharply again at Salt Rock, where both were maximal. Abundances at west coast sites were comparable to those recorded in this region by Hammond & Griffiths (2002), but considerably lower than those reported by Hockey & van Erkom Schurink (1992) and Griffiths *et al.* (1992). The number of species recorded per location varied from a maximum of 42 at Port Elizabeth and Port St Johns to a minimum of 21 at Gansbaai (Table 2). This compares with the 35 species recorded by Hammond & Griffiths (2002), but is considerably lower than the 68 species recorded from *M. galloprovincialis* beds and 69 from *A ater* beds by Griffiths *et al.* (1992). All these studies took place in the same region, used the same sampling technique and processed similar numbers of replicate samples. Comparisons with other studies are confounded not only by biogeographical differences, but also by effects of number and size or samples taken, the size resolution to which samples were sorted and the level of taxonomic resolution available, all of which can profoundly effect species counts.

The diversity and richness indices of the faunal community remained fairly constant around the coast, except at the extremes of the distribution, at Swakopmund and Salt Rock, where both measures were significantly reduced. Interestingly, these are the very sites showing maximal faunal abundance, indicating that samples in these areas were dominated by relatively few species (most importantly the holothurian *Pseudocnella sykion* at Swakopmund and the barnacle *Tetraclita serrata* at Salt Rock – see Table 3).

Based on these mussel-bed faunal data, the established Namib, Namaqua, Agulhas and Natal biogeographical provinces, as recognized by Emanuel *et al.* (1992) and later authors, still emerge (Fig. 2). The implication of this finding is that these provinces remain evident even within a physically relatively homogenous environment (a mussel matrix) and are not simply the result of changes in habitat type (for example the replacement of kelp beds in the west by turf algae and coral reefs in the east). Despite the fact that these biogeographic distinctions can be made, a few dominant species, notably *Aulactinia reynaudi, Pseudonereis variegata, Scutellastra granularis* and *Tetraclita serrata* characterize the mussel-bed fauna across a wide range of sites, in terms of abundance and/or biomass. Relatively few species are characteristic of one or a few sites, such as *Discinisca tenuis* and *Pseudocnella sykion* at Swakopmund, and *Nucella cingulata,* at Groenrivier (Tables 3 & 4).

These results thus confirm that the mussel matrix supports a rich and diverse macrofaunal community, and that this differs in composition around the coastline. The contribution this mussel community makes to the biodiversity and economy of the shore as a whole depends, of course, on what proportion of the shore is covered in mussels. Along the South African coast these proportions have undergone marked changes over the past few decades. In particular the invasion of *M. galloprovincialis* on the west and southwest coasts (van Erkom Schurink & Griffiths 1990; Robinson *et al.* 2005) has resulted in massive increases in overall mussel biomass and cover, as well as an upward movement of the mussel zone, in these regions. As these dense mussel beds have replaced large areas of relatively open rock, primarily dominated by limpets, overall intertidal invertebrate biomass, density and species diversity have increased dramatically, each square metre of mussels bringing with it not only 20–50 kg of mussel biomass, but also a further 5000 or more macrofaunal invertebrates with an additional biomass of 2 kg or more (Table 2).

On Eastern Cape and KwaZulu-Natal coasts the reverse process is taking place, due to extensive exploitation of the brown mussel, *P. perna* (Hockey & Bosman 1986; Lasiak & Dye 1989). This has not only severely depleted the resource, but has tended to push the 'centre of gravity' of the mussel beds progressively down-shore, such that only small clumps of mussels remain scattered on the lower shore and sublittoral fringes (Van Erkom Schurink & Griffiths 1990). As a result the upper and mid-littoral zones have become overgrown by macroalgae (Dye 1995). Other studies have shown that the recovery of *P. perna*-dominated communities is poor, as the species of articulated coralline algae, which colonize the substratum soon after an area has been cleared of mussels, still persist as the major space occupiers even years later (Lambert & Steinke 1986).

This loss of mussel cover and biomass is likely to have deleterious effects on the large number of macrofaunal species that previously relied on the mussel-bed habitat for food and shelter. This is evident in our data (Tables 1 & 2) in that mussel cover, biomass and bed depth in the most intensively exploited region is now extremely low and that the remaining mussels support an exceptionally low infaunal abundance and biomass. The wider implications of these longer term changes in mussel-bed community structure to the economy of the shore, for example in terms of loss of food for shore birds and other predators, may be profound, but remain to be investigated.

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